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AGGRESSIVE FUNCTION AND INDUCED DEVELOPMENT OF CATCH TENTACLES IN THE SEA ANEMONE *METRIDIUM SENILE* (COELENTERATA, ACTINIARIA)

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Catch tentacles, found near the mouth in some individuals of the sea anemone *Metridium senile*, are more opaque than the regular tentacles and conspicuously larger. In anemones about 6 cm in expanded column height, representative dimensions of the regular tentacles are 0.5 × 7.0 mm, while noninflated catch tentacles measure about 3.0 × 20.0 mm. Catch tentacles are capable of expanding to several times their resting length and breadth, reaching dimensions of 5.0 × 120.0 mm. When thus expanded, a catch tentacle repeatedly extends and retracts, touching its tip to the substratum. These movements were first mentioned by Gosse (1860) in several British anemones. Carlgren (1929) named the large, inflatable tentacles *Fangtentakeln* and showed them to have a different cnidom from the other tentacles of the anemone in the species *Diadumene cincta, D. neozelanica,* and *D. kameruniensis.* Catch tentacles are now known to occur in at least some species in six families of acontiate anemones: Diadumenidae, Sagartiidae, Metridiidae, Isophelliidae, Sagartiomorphidae, and Haliplanellidae (Williams, 1975).

The catch tentacles in specimens of *Metridium senile* from the central California coast were described by Hand (1955). He reported that specimens with catch tentacles formed less than one per cent of the intertidal populations, did not occur as isolated individuals, and showed no obvious pattern in their distribution. He found the catch tentacles to have a strikingly different cnidom than the regular tentacles. The main thrust of Hand's work was taxonomic, and the few observations he made on the activities of catch tentacles suggested they might aid in feeding.

Williams (1975), in studies on *Haliplanella luciae* and *Diadumene cincta*, found that food and other materials did not adhere to the catch tentacles and that the tentacles were not brought to the mouth. Williams cited observations of P. R. G. Tranter of the Plymouth Marine Laboratory that in the anemones *Cereus pedunculatus, Sagartia elegans* and *S. troglodytes,* the catch tentacles were used offensively against members of their own species from different localities and against other species. When the tip of an expanded catch tentacle contacted another anemone, it adhered to it; later the catch tentacle formed a constriction and broke here, leaving its tip attached to the victim. The catch tentacles of these species did not adhere to food. Williams (1975, p. 244) further noted that "*Metridium senile* and *Diadumene cincta,* although possessing catch tentacles, were not observed exhibiting aggressive behavior by Tranter."

Metridium senile reproduces asexually by pedal laceration (Stephenson, 1935), thus forming clones of a few to many hundreds of individuals. Clonemates are

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remarkably alike and are easily distinguishable from members of other clones by body color, most commonly white or various shades of brown, and by the presence or absence of a pattern of white banding on the bases of the tentacles. Clones are formed in the anemone *Anthopleura elegantissima* by fission and individuals exhibit aggressive behavior toward members of other clones (Francis, 1973a, b).

The purpose of the present study is to re-examine catch tentacle function in *Metridium senile.*

Materials and Methods

This study was conducted at the Hopkins Marine Station of Stanford University, from September, 1975, through January, 1976. Extensive populations of *M. senile* grow nearby on the pilings of Wharf No. 2, Monterey, California. Field observations and collections were made using SCUBA gear. Specmens returned to the laboratory were kept in plastic pans provided with running sea water at 12–13° C, each pan containing only members of one clone. Experiments were conducted after the anemones had attached by the pedal disc and had expanded the tentacle crown, usually 24–48 hours after collection. Anemones were used in behavioral observations for one week. The anemones observed ranged in size from approximately 5 to 10 cm in expanded column height.

Details of experimental protocols accompany the description of each experiment in Results.

Results

Responses to food

To determine if *Metridium senile* uses its catch tentacles in feeding, living crustaceans (the copepod *Tigriopus californicus* and larvae of the brine shrimp *Artemia salina*), were offered as food. Individual prey animals were held by the abdominal segments with fine forceps. Prey animals were touched first to a catch tentacle, secondly to a regular tentacle, and thirdly to a catch tentacle. The same procedure was followed in fifteen animals in which one or more catch tentacles were inflated, touching the prey animal to both inflated and resting catch tentacles, and in fifteen in which the catch tentacles were not inflated. Each prey animal captured was replaced by another.

In no case did the catch tentacles adhere to the food offered, whereas it was always captured by the regular tentacles. When touched with a prey animal, the catch tentacles retracted slightly, just as they responded to similar touches with a clean probe. Not only did the prey animals not adhere to the catch tentacle, but they were able to swim away after repeated contacts with the sides and tip of a catch tentacle. In contrast, prey animals presented to the regular tentacles immediately became attached to the tentacle and were immobilized. The tentacle contracted, and with others surrounding it, curled and bent toward the mouth where the prey was ingested. Following active feeding involving regular tentacles, the catch tentacles still did not capture prey animals. Only once did a detrital particle adhere to an expanded catch tentacle. It was not delivered to the mouth and later came free.

These observations show that the catch tentacles of *Metridium senile* are not used in feeding. They did not capture prey and did not exhibit any of the characteristic feeding movements of the other tentacles.

Distribution of individuals with catch tentacles within local populations

Considering the possibility that catch tentacles might be used offensively against nonclonemates, the distribution of specimens of *Metridium senile* with catch tentacles was reinvestigated. The dense subtidal populations at depths of approximately 2 to 25 feet on wharf pilings at Monterey provided the most favorable units for study. Preliminary observations indicated that specimens of *M. senile* with catch tentacles were usually found along the margins of clones opposing different clones. This was documented by a series of color photographs of twenty-five clones showing the following three types of sites: first, the borders of clones where individuals of one clone were situated within approximately 10 cm (the length of an expanded catch tentacle) of anemones of another clone; secondly, the centers of clones, where anemones were surrounded by clonemates and were not within reach of individuals of other clones; and thirdly, the edges of clones where the outermost anemones those without catch tentacles were counted in all photographs for each of the three were not within reach of individuals of a different clone. Anemones with and types of sites (Table I).

Specimens of *Metridium senile* with catch tentacles are conspicuously abundant at borders separating adjacent clones, and very scarce elsewhere. While 22.6% (355/1523) of the 1523 anemones examined possessed catch tentacles, this is not an unbiased estimate of the abundance of anemones with catch tentacles in the entire population, because greater attention was focused on the borders where members of two clones were in near contact. Of those anemones with catch tentacles, 96% (339/355) were at these borders, and 77% (339/441) of the border anemones had catch tentacles. Border anemones lacking catch tentacles were usually the smallest individuals. G-tests (Sokal and Rohlf, 1969) showed no significant differences between numbers of individuals with catch tentacles at the centers of clones and those at the edges of clones where there was no contact with nonclonemates. In contrast, differences between numbers of individuals with catch tentacles in border and nonborder (center plus edge) areas were highly significant ($P < 0.005$).

TABLE I

Distribution of specimens of M. senile *possessing catch tentacles, with respect to their positions within clones.*

	Number of anemones	
Positions of anemones	With catch tentacles	Total observed
At clone margin bordered by another clone	339	441
At center of clone	11	857
At clone edge not adjacent to another clone	5	225
	355	1523

The separation of clones can be quite marked, with an anemone-free zone 7–12 cm wide extending between the clones, and with specimens bearing catch tentacles lining the borders (Fig. 1). In other cases different clones occur in close proximity with no distinct anemone-free border zone, but neighboring members of both clones possess catch tentacles. This is the case where a small number of anemones of one clone are found surrounded by members of a larger clone. Among the 1523 anemones enumerated, only eleven anemones with catch tentacles were seen in the centers of clones where no adjacent nonclonemate could be identified.

Many specimens of *M. senile* have catch tentacles where clones of *M. senile* and *Anthopleura elegantissima* meet at intertidal levels on the pilings. The two species are not separated by a wide anemone-free zone.

In summary, field observations indicate that specimens of *Metridium senile* with catch tentacles occur in circumstances where nonclonemates are in close proximity. This suggests the occurrence of catch tentacles may be determined by the presence of nonclonemates.

Behavioral studies on the role of catch tentacles

The facts that catch tentacles in *Metridium senile* are not used in feeding and that they occur predominantly in individuals along borders separating two different clones suggest that they function in aggression against genetically different anemones. Field and laboratory observations were made to ascertain whether aggression is exhibited.

Catch tentacles were first observed in undisturbed natural populations to get indications of their use. In the field, an occasional anemone was seen with one or more catch tentacles inflated and moving with the current. When the sides and tip of the inflated tentacle of one anemone brushed any body surface of its clonemates, there was no response by either anemone. When the catch tentacle tip contacted a nonclonemate, approximately 1 cm of the tip attached to the nonclonemate, which contracted locally. The catch tentacle remained attached and after two to five minutes began to withdraw and deflate, breaking about 1 cm behind the tip. This sequence was sometimes repeated with another catch tentacle on the same anemone. Of the numerous catch tentacles observed expanded in the field during the course of the study, only five instances of contact with nonclonemates were witnessed.

More detailed studies of catch tentacle behavior were carried out in the laboratory. Anemones with and without catch tentacles, collected from several clones, were kept in holding pans in the laboratory. Studies were made of the behavioral interactions between over forty pairs of clonemates and fifty pairs of nonclonemates, including some in which *Metridium senile* was paired with *Anthopleura elegantissima*. Interactions between pairs were recorded in the following laboratory situations: undisturbed anemones in pans containing members of only one clone, and in pans containing anemones of more than one clone; and anemones settled on movable glass squares. In the latter case, expanded anemones were gently moved so that the tips of the feeding tentacles of the two animals were either just out of contact (and allowed to contact naturally), or they were carefully moved so that the anemones experienced tentacle-tip contact. No differences in behavior were seen which appeared attributable to the method by which initial tentacle con-

FIGURE 1. Two adjacent clones of *M. senile* on a wharf piling at Monterey, California. The clones are separated by an open corridor bordered by anemones with catch tentacles. Scale bar equals 3 cm.

tact was established by the pair. Anemones on glass squares were out of contact with all other anemones for a period of at least an hour.

Results of the experiments are summarized in Table II and Figure 2, while Figure 3 illustrates a typical sequence of behavior between two nonclonemates with catch tentacles following mutual contact of feeding tentacle tips. In all cases of clonemate and nonclonemate contact, both anemones responded to this contact with slight withdrawals of the tentacles touched, and a slight swelling of these and other feeding tentacles particularly in the area of contact. Tentacle retractions of both anemones were more pronounced upon contact between nonclonemates and were especially violent when specimens of *M. senile* contacted other species (*e.g., Anthopleura elegantissima*).

After numerous feeding tentacles had made mutual contact (Fig. 3A), each individual of the pair of *M. senile* began bending its column, first away from, and then toward, the area of contact with the other anemone (Fig. 3B). This bending brought the feeding tentacles of the two animals repeatedly in and out of contact. The period of bending varied from ten minutes to four hours, but typically lasted about twenty minutes.

TABLE II

The behavioral interactions following contact between the tips of feeding tentacles in anemone pairs, including individuals with and without catch tentacles (CT) in paired clonemates, paired nonclonemates, and M. senile (M.s.) *paired with* Anthopleura elegantissima (A.e.). *Behavior of each pair is followed through each distinguishable unit of the interaction. Anemones had been out of contact with all others for at least an hour. Ratios represent the number of pairs in which a positive response was recorded out of the number of pairs tested. An asterisk marks each case where an inflated catch tentacle was made to contact another anemone without previous feeding tentacle tip contact.*

Features of the behavioral interaction	Responses of anemones of interacting pair							
	M.s., clonemates			*M.s.* nonclonemates			*M.s. vs. A.e.*	
	Both without CT	a) With CT b) Without CT	Both with CT	Both without CT	a) With CT b) Without CT	Both with CT	*M.s.* without CT	*M.s.* with CT
Tentacles retract on tentacle tip contact between pairs members	5/5	a) 6/6 b) 6/6	20/20	5/5	a) 5/5 b) 5/5	25/25	*M.s.* 3/3 *A.e.* 3/3	*M.s.* 6/6 *A.e.* 6/6
Column bends following the above	5/5	a) 6/6 b) 6/6	20/20	5/5	a) 5/5 b) 5/5	25/25	*M.s.* 3/3 *A.e.* inflates acroraghi	*M.s.* 6/6
Regular tentacles applied to tentacle crown of other anemone	0/5 —	a) 0/6 b) 0/6	0/20	5/5	a) 0/5 b) 0/5	1/25	*M.s.* 3/3 *A.e.* 0/3	*M.s.* 0/6 *A.e.* 0/6
Catch tentacles expand	—	a) 6/6 b) —	16/20	—	a) 5/5 b) —	25/25	—	*M.s.* 5/6 *A.e.* —
Catch tentacle adheres to other anemone upon contact	—	a) 0/6 b) —	0/16 *0/10	—	a) 5/5 b) —	25/25 *10/10	—	*M.s.* 5/5 *A.e.* —
Victim's catch tentacles subsequently expand	—	—	0/16 *0/10	—	—	24/25 *10/10	—	—
Injury incurred	None	a) None b) None	None	Slight necrosis	a) None b) Necrosis	Necrosis	Necrosis	*M.s.* none *A.e.* necrosis

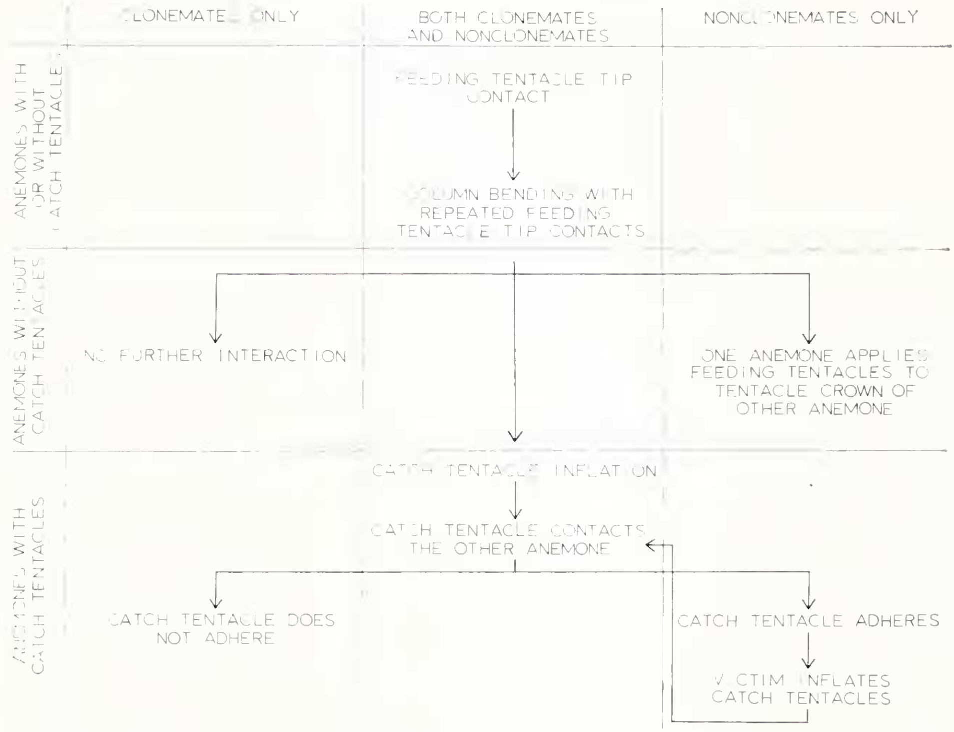

FIGURE 2. Pattern of behavioral units in anemone pair interaction following feeding tentacle tip contact between pair members which had not been in contact with other anemones for an hour or more. Pairs include individuals of *M. senile* with and without catch tentacles *versus* clonemates and nonclonemates with or without catch tentacles.

Of anemones without catch tentacles, clonemates ceased notable interaction at this point; they stopped bending and either remained in contact, or moved away. The bending behavior was observed in clonemates which had been separated from contact with other members of their clone for a period of hours. In nonclonemates, however, the column-bending became more exaggerated. Eventually, one of the pair brought a large portion of its tentacle crown down on the upper surface of the tentacle crown of the second anemone. This action was sometimes repeated. The second anemone ceased column bending and later showed slight necrosis on its tentacles. Following the encounter, one or both anemones moved out of contact.

Where one or both members of a pair, either clonemates or nonclonemates, of *M. senile* had catch tentacles, catch tentacle inflation always followed the period of bending with repeated feeding tentacle tip contacts (Fig. 3C). Usually only one, and sometimes two, catch tentacles inflated per individual. Most frequently, the catch tentacles of one indvidual inflated and contacted the second anemone before the second inflated its catch tentacles. Nearly simultaneous catch tentacle inflation in both anemones did sometimes occur. Inflated catch tentacles displayed considerable activity, extending and partially retracting, while repeatedly touching the tip to the surroundings.

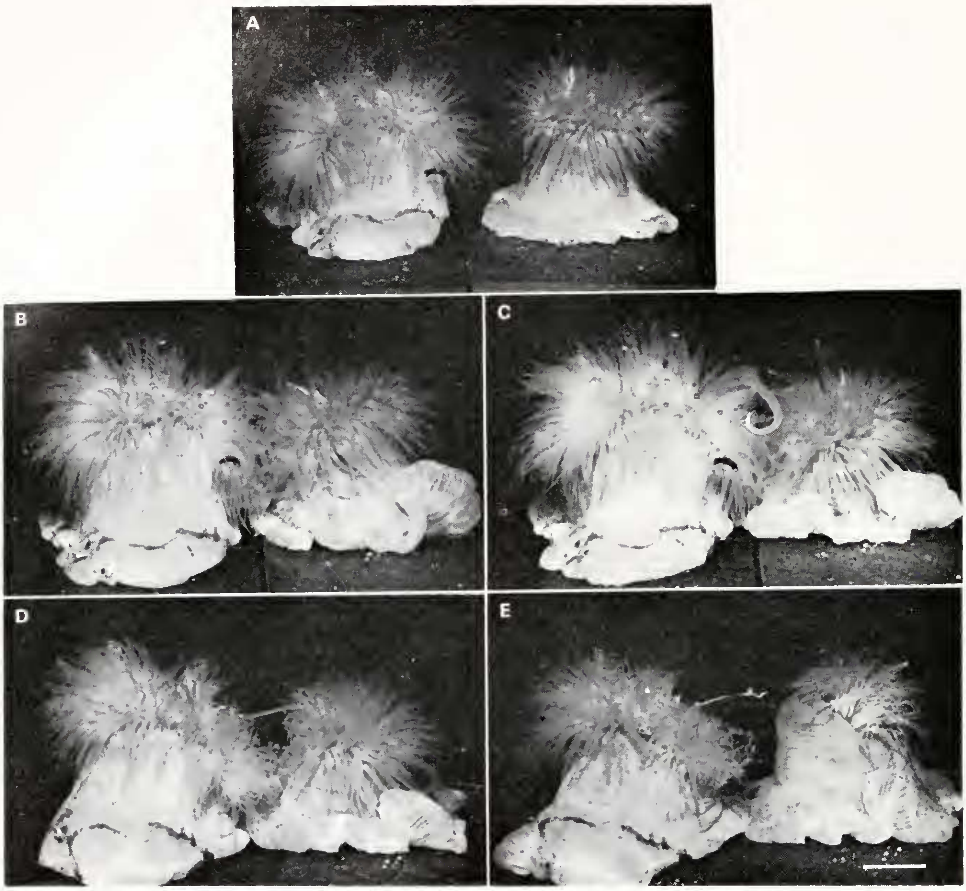

FIGURE 3. Sequence of behavior in two nonclonemates of *M. senile*, both with catch tentacles: a) feeding tentacle tips have come into contact; the white tips of two noninflated catch tentacles are visible in the anemone on the right, which begins to bend away from the point of contact; b) the anemone on the right now bends the column toward the site of initial contact; repeated column-bending motions of both anemones lead to repeated contacts of the feeding tentacles; c) an inflated catch tentacle from the anemone on the left has attached at several points, near and at its tip, to tentacles of the individual on the right, in which several catch tentacles are inflating; d) the attached catch tentacle of the left anemone has begun to deflate and withdraw; the victim on the right shows partial contraction of the tentacles in the area of catch tentacle adhesion; e) the catch tentacle of the left anemone has broken contact. The victim on the right has strongly contracted and is inflating several white-tipped catch tentacles. Scale bar equals 1.5 cm.

When the catch tentacle tip contacted a clonemate, no reaction by either anemone was observed. The catch tentacle often remained in contact with the clonemate for several minutes: it moved the tip over the clonemate's column, base, and tentacles, but it never adhered and eventually withdrew and deflated. The clonemates observed had been out of tentacle contact with other clonemates for a period of at least an hour.

When an expanded catch tentacle contacted a nonclonemate on either the tentacle crown or column, about 1 cm of the catch tentacle tip immediately adhered. The victim contracted sharply near the site of attachment, but did not withdraw completely. The aggressor sometimes moved the inflated unattached portion of the catch tentacle, enabling sites further from the tentacle tip to attach to the victim (Fig. 3C). After two to five minutes, the catch tentacle began to pull back and deflate (Fig. 3D), leaving the attached portions of the catch tentacle adhering to the victim. An obvious constriction sometimes formed 1 cm behind the tip, where breakage subsequently occurred (Fig. 3E).

In encounters between two nonclonemates both possessing catch tentacles, an attack by a catch tentacle of one animal led to the immediate expansion of the victim's catch tentacles (Fig. 3C, E). This inflation of one, or frequently several, catch tentacles took place in one to five minutes, sometimes while the aggressor's catch tentacle was still attached. In experimental situations where an inflated catch tentacle was made to contact a nonclonemate without previous mutual feeding tentacle contact between the two animals, the victim's catch tentacles also inflated. Up to nine successive attacks by one specimen of *M. senile* upon another were observed, each attack involving a different catch tentacle. More usually one to three attacks were made by each individual of a given pair of nonclonemates. One or both anemones eventually moved away. In all cases severe necrosis ensued where the catch tentacle tips remained attached to a victim, and in three anemones death followed several days later.

Anemones well separated from any contact with others sometimes inflated a catch tentacle. The stimulus for this is not known. On the other hand, the pedal discs of clonemates and nonclonemates were sometimes observed to be in contact for many hours without the catch tentacles ever inflating. In no case was a contact between pedal discs, or between the tentacles of one animal and the base of another, associated with catch tentacle inflation.

Contact of a catch tentacle tip with any portion of a genetically different anemone resulted in adherence of the tip and in contraction of the victim at the site of adherence, indicating nematocyst discharge from the catch tentacle tip. Catch tentacle contact with clonemates showed no indication of any nematocyst discharge.

Inducing the formation of catch tentacles

The occurrence of catch tentacles in individuals of *Metridium senile*, residing adjacent to nonclonemates of *M. senile* or to other anemones such as *Anthopleura elegantissima*, suggests that formation of catch tentacles is induced by contact between different anemones. In two clones separated by over 30 cm, no anemones had catch tentacles, except where a wanderer from one clone had come to rest next to the other clone. Four anemones immediately adjacent to the wanderer had several catch tentacles each. What appeared to be partially developed catch tentacles were seen in the field; the outermost anemones in a clone had numerous large and very opaque catch tentacles and the next few more central anemones had fewer, smaller, and more transparent catch tentacles.

When an anemone bears catch tentacles, these always occur in the one or two circles of tentacles nearest the mouth. The nematocysts of catch tentacles are strikingly different from those in the feeding tentacles. Holotrichs, atrichs, and microbasic amastigophores are found in catch tentacles. Spirocysts, and microbasic a and *b*-mastigophores constitute the bulk of the nematocysts in the feeding tentacles, with some basitrichs found near the bases of the tentacles (Hand, 1955).

In order to test the hypothesis that contact with nonclonemates induces formation of catch tentacles, seven individuals without catch tentacles were selected from each of two clones and were kept in running sea water in a small aquarium ($14 \times 14 \times 10$ cm). Under these crowded conditions, frequent tentacle contacts between nonclonemates were inevitable. Counts of the major types of nematocysts were made at the beginning of the experiment and after four, six, and nine weeks, in tentacles distant from the mouth, tentacles in the first circle surrounding the mouth which appeared unchanged, and tentacles of the first circle in which opacity increased. Tentacles were removed by grasping them near the base with fine forceps and pulling lightly, causing the tentacle to come free where joined to the oral disc. Tentacles were mounted in sea water on slides under a coverslip and gentle pressure applied to yield an even squash preparation. Preparations were examined at $1000\times$ magnification. Differential counts of nematocyst types were made in five arbitrarily selected fields representing both the tip and base of the tentacles (Fig. 4, Table III).

A slight opacity of one first-circle tentacle was noticed in one individual after one week, and in four of the seven members of the same clone at two weeks. Visible signs of catch tentacle formation in some members of the second clone occurred after four weeks. At nine weeks, eleven of the fourteen individuals possessed catch tentacles. The number of catch tentacles per individual ranged from two to thirteen.

Figure 4 shows the loss of feeding tentacle nematocysts and the acquisition of catch tentacle nematocysts in developing catch tentacles over the nine-week confinement of two clones. Counts were made of the nematocysts: at four weeks, in one tentacle in each of three individuals of one clone; at six weeks, in one tentacle in each of seven individuals from both clones; and at nine weeks in one or two tentacles in all eleven anemones which possessed catch tentacles. In Table III, counts made at zero and nine weeks of the cnidoms of feeding tentacles, both close to and far from the mouth, and of the cnidoms of fully developed catch tentacles, are compared to cnidom counts in the tentacles nearest the mouth which increased in capacity in the confined clones at week nine. Counts were made of nematocysts in two feeding tentacles taken close to the mouth, and two taken far from the mouth, in each of four individuals in each clone at zero and nine weeks. The nematocyst types were counted in two fully-developed catch tentacles taken from each of four members of one experimental clone which already bore catch tentacles at week zero. The proportions of nematocyst types given in Figure 4 and Table III are all averages of counts taken at the tips and bases of the tentacles.

In the experimental animals, the mean percentages of the nematocyst types in the feeding tentacles (both peripheral tentacles and those nearest the mouth) did not vary substantially during the nine weeks; spirocysts constituted approximately 80% of the cnidom. Some tentacles in the first circle around the mouth showed an increasing opacity first near the tip, and later over the entire tentacle; this was accompanied by an increase in the length and width of the tentacle. Tentacles undergoing this change invariably contained catch tentacle nematocysts (atrichs and holotrichs) in varying stages of development, in addition to nematocysts char-

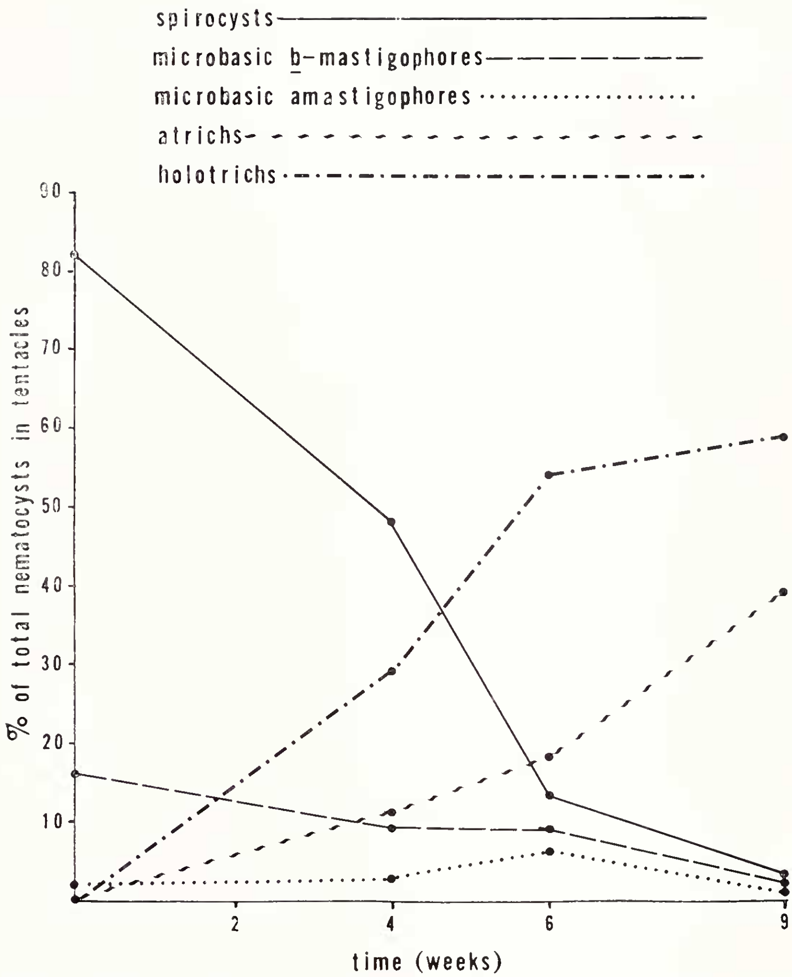

FIGURE 4. Average proportions of the several nematocyst types in tentacles of *M. senile*. Seven anemones without catch tentacles from each of two clones were confined for nine weeks such that frequent feeding tentacle contact was inevitable. Nematocyst counts were made of tentacles nearest the mouth at the time of first interclonal contact; the counts were repeated after four, six, and nine weeks in those tentacles nearest the mouth which showed visible increases in opacity. Data points are indicated with solid circles.

acteristic of feeding tentacles. The proportion of catch tentacle nematocysts increased throughout the nine weeks, as spirocysts and *b*-mastigophores declined in numbers and disappeared (Fig. 4). The proportions of the major nematocyst types in feeding tentacles (spirocysts and *b*-mastigophores) and in catch tentacles (atrichs and holotrichs) in the experimental animals were compared between week 0 and week 9 in a Kendall Rank Correlation test (Sokal and Rohlf, 1969). The test gave a highly significant negative correlation, with $P < 0.001$. The proportions of different types of nematocysts in the developing catch tentacles after

Table III

Average proportions of the several nematocyst types in tentacles of M. senile. *Nematocyst counts were made of fully developed catch tentacles in individuals of one clone at week 0. Seven members of this clone and seven from a second clone, all lacking catch tentacles, were confined for nine weeks where frequent feeding tentacle contacts were inevitable. The average percentages of nematocyst types in the tentacles nearest the mouth and in peripheral tentacles are given at week 0 and week 9.*

Nematocyst type	Tentacle type					
	Catch tentacles	Tentacles nearest the mouth			Peripheral feeding tentacles	
	Week 0	Week 0	Showing increased opacity At week 9	Not showing increased opacity At week 9	Week 0	Week 9
Spirocysts	0%	82%	0%	81%	82%	84%
Microbasic *b*-mastigophores	0	16	0	17	16	14
Microbasic amastigophores	1	2	2	2	2	2
Atrichs	40	0	39	0	0	0
Holotrichs	59	0	59	0	0	0

nine weeks of growth closely approach those found in fully formed catch tentacles in animals collected from the field (Table III).

Several tentacles in the first circle surrounding the mouth in a majority of individuals from the two clones developed into functional catch tentacles. The time of first appearance and the number of catch tentacles formed varied between clones and between individuals in the same clone. The transformation of feeding tentacles into catch tentacles, including the dramatic change in nematocyst types, was nearly completed in nine weeks. Catch tentacles were inflatable after three to four weeks of growth, at which time all nematocyst types were present. Numerous interclonal attacks occurred with severe injury inflicted. Studies on catch tentacle induction are continuing.

Discussion

Evidence presented in this study for *Metridium senile* and by Williams (1975) for *Haliplanella luciaea, Diadumene cincta, Cereus pedunculatus, Sagartia elegans,* and *S. troglodytes,* shows that in these species the catch tentacles function in inter- and intraspecific aggression and not in feeding, as had been previously assumed. Considering these findings, the term "catch tentacle", implying a food-gathering function, is misleading. On present evidence a more appropriate functional name would be "fighting tentacle", in contrast to the smaller tentacles whose primary function is feeding. If future research on the other species with similar tentacles shows also function in aggression, renaming catch tentacles should be considered.

The catch tentacles are labile structures in *M. senile,* occurring where non-clonemates are adjacent. This study demonstrated their induction from regular feeding tentacles in individuals lacking catch tentacles during interaction with non-clonemates over several weeks. This externally triggered induction involves the development of a new set of nematocysts and a system for their continued production, a corresponding change in morphology, and the emergence of the behavior appropriate for implementation of the aggressive structures. Some interaction is needed to maintain the induced structures and behavior, for Hand (1955) described catch tentacle regression in isolated individuals.

The aggression between nonclonemates of *Metridium senile* is analogous to that described for *Anthopleura elegantissima* by Francis (1973a), with interesting parallels. In both species tentacle tip contact with nonclonemates stimulates aggression. The development of structures used in aggression is greatest in individuals most likely involved in aggression. Francis (1976) found that individuals of *A. elegantissima* at inter-clonal borders had more and larger acroraghi (which function is aggression) than other clonemates.

The aggressive ability of each anemone species and each clone probably has a profound effect on the competition for space. Lang (1973) showed that interspecific aggressive interactions were critical in the development of community structure in scleractinian corals. Depending on the species' position in an invariable hierarchy of aggressiveness, aggression prevented a colony from being overgrown by another species, or enabled one species to overgrow others. Rogers (Hopkins Marine Station, unpublished report) demonstrated a hierarchy in aggressiveness among four clones of *Anthopleura elegantissima*. Where several species of anemones co-occur, aggression may be an important determinant in their distributions. This is suggested by Chao (Hopkins Marine Station, unpublished report), who showed that a hierarchy of aggressiveness exists among three species of anemones whose populations co-occur but do not intermingle at Monterey Wharf #2: *Metridium senile,* tested without catch tentacles, was most aggressive, followed by *Corynactis californica,* and finally by *Anthopleura elegantissima.*

Each anemone clone, consisting of genetically identical individuals, is comparable to an organism upon which natural selection is acting. The more space occupied by the clone, the greater the available area for food capture. This should allow the clone to expand more rapidly by asexual means, resulting in a larger number of sexually reproducing individuals. Thus, the aggressive ability of the clone, being critical in maintaining and expanding its area, would seem to be of substantial adaptive value.

My sincerest thanks go to Dr. Donald Abbott and Charles Baxter, who contributed immeasurably to every aspect of this study. Christopher Kitting kindly took the photographs on which field data were based and those documenting behavior. I appreciate the comments made upon the manuscript by Dr. James Case and Dr. Demorest Davenport. I also wish to thank Dr. Cadet Hand for his suggestion that I re-examine catch tentacle function in *Metridium senile.*

Summary

1. The "catch tentacles" of *Metridium senile* are larger and more opaque than normal feeding tentacles, are capable of great enlargement, and possess a cnidom differing strikingly from that of the regular or feeding tentacles.

2. The catch tentacles are not used in food capture. Inflated or resting catch tentacles never accepted food in animals which were feeding with regular tentacles.

3. Genetically different clones of *M. senile* are often separated by narrow open corridors free of anemones. Specimens of *M. senile* bearing catch tentacles are found along the borders of these corridors, and in most situations where individuals of different clones are adjacent and within reach of one another.

4. Catch tentacles are used in both intra- and interspecific aggression. Prolonged and repeated feeding tentacle contact between nonclonemates and clonemates where the individuals have been isolated from contact with all other anemones for a period results in the expansion of catch tentacles. Catch tentacle expansion sometimes occurs without an apparent stimulus. Nematocyst discharge of the catch tentacle tip occurs only upon contact with a genetically different individual. After contact and discharge the catch tentacle breaks, leaving about 1 cm of the tip attached to the victim; necrosis at this site follows, and occasionally the victim dies.

5. Catch tentacle formation in individuals lacking them was observed in members of two clones which were confined in close quarters for nine weeks. Feeding tentacles closest to the mouth became enlarged and more opaque, lost their feeding nematocysts and developed nematocysts characteristic of catch tentacles. The transformation was largely completed in nine weeks.

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